TOWARD A PHYLOGENY OF *MIMOSA* (LEGUMINOSAE: MIMOSOIDAE): A PRELIMINARY ANALYSIS OF SOUTHERN SOUTH AMERICAN SPECIES BASED ON CHLOROPLAST DNA SEQUENCE[1]

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Abstract

The pantropical and subpantropical genus *Mimosa* L. comprises more than 500 species, of which nearly 480 are reported for the American Continent. *Mimosa* is subdivided into five sections, four of which are represented in southern South America: *Batocaulon* DC., *Habbasia* DC., *Calothamnos* Barneby, and *Mimosa*. Previous taxonomic studies of the species from the austral region have found classification conflicts among (a) sections *Batocaulon* and *Habbasia*, (b) sections *Calothamnos* and *Mimosa*, and (c) series and subseries within section *Mimosa*. This paper reports a preliminary phylogenetic analysis of chloroplast nucleotide sequences of the *trnL* intron and the *trnL-trnF* intergenic spacer from 34 species of *Mimosa* and related genera. Key morphological characters were mapped onto the phylogenetic hypothesis and discussed. Sequence analysis indicates that the genus *Mimosa* is monophyletic; it is derived from *Piptadenia viridiflora* (Kunth) Benth. The four sections proposed by Barneby are not natural groups. The cladogram retrieved indicates that the representatives of *Mimosa* sect. *Batocaulon* are not clustered, the xerophylous representatives of this section are basal, and the remaining species are related to those species of section *Habbasia*, suggesting that section *Batocaulon* ser. *Stipellares* is more recently derived. The species of *Mimosa* sect. *Calothamnos* that were analyzed are nested in section *Mimosa*. The results seem to support retention of this section within section *Mimosa* as was noted previously by Bentham. The chloroplast sequence data suggest that the representatives from sections *Calothamnos* and *Mimosa* share a common ancestor with those from section *Habbasia* and section *Batocaulon* ser. *Stipellares*.

Key words: cpDNA, *Mimosa*, phylogeny, *trnL* intron, *trnL-trnF* intergenic spacer.

The pantropical and subpantropical genus *Mimosa* L. has about 500 species. Nearly 480 are reported for the American Continent (Barneby, 1991, 1993; Turner 1994a, b; Fortunato & Palese, 1999; Queiroz et al., 1999; Grether, 2000; Silva & Secco, 2000; Izaguirre & Beyhaut, 2002). The first comprehensive taxonomic revision of this diverse genus was proposed by Bentham (1875) in his global monograph of the Mimoseae and later supplemented in *Flora Brasiliensis* (1876). Bentham (1841–1842, 1875) recognized in the genus: (a) section *Mimosa*, with haplostemonous flowers; and (b) *Habbasia* DC., with diplostemonous flowers, each organized into infrasectional ranks. The generic definition of *Mimosa* as proposed by Bentham has found nearly universal acceptance. Its limits were only challenged by Britton and Rose (1928) in *North American Flora*, with the introduction of a novel division. They segregated *Mimosa* as another genera based on species that had different pod type and leaf reduction (= phyllodes). However, their artificial classification has largely been ignored. In South America, the only revision of the Argentinean species was published by Burkart (1948). His treatment was largely in accord with Bentham's infrageneric classi-

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fication, even though eight additional species and seven varieties were described.

Although there has been no global evaluation of *Mimosa* since Bentham (1875, 1876), Barneby (1991) presented a new taxonomic treatment of *Mimosa* in the New World that makes up approximately 90% of the total species. He noted two chief foci of speciation in the Americas: (a) Brazil south of Amazonia and adjacent areas of Paraguay, Argentina, and Uruguay; and (b) central and southern Mexico, as well as other minor ones in Cuba-Hispaniola, and the Orinoco basin. In addition to this, Barneby expanded Bentham's generic definition, but he also included the genera *Schrankia* Willd. and *Schranckiastrum* Hassl. He reorganized the sectional and infrasectional classification, established new categories, and reordered the old ones. This classification recognized five sections in *Mimosa*: *Mimadenia* Barneby, *Batocaulon* DC., *Habbasia*, *Calothamnos* Barneby, and *Mimosa* (Table 1).

In the phylogeny proposed by Barneby, *Mimosa* was derived from Piptadenioid ancestors (Barneby, 1991: 15–16). He suggested that section *Mimadenia* is a morphological group intermediate between the Piptadenioid ancestor and the remaining species of *Mimosa*. The novel position he gives to section *Mimadenia* is based on the extra floral nectaries that resemble both genera, and the ovate anthers that are intermediate between the orbicular connective, girdled by incurved anther sacs of *Mimosa* and the oblong connective, which is flanked by straight parallel anther sacs of *Piptadenia* Benth. The anthers of the species of *Mimosa* sect. *Mimadenia* always lack the terminal gland present in *Adenopodia* C. Presl and *Piptadenia*. The craspedium type of some species of *Mimosa* sect. *Mimadenia* is not different from that of *Adenopodia* and *Entada* Adans., but is not related to the valvate pod present in *Piptadenia* s.l. (Barneby, 1991: 25).

All diplostemonous species of *Mimosa* were included in section *Habbasia* and divided by Bentham (1875) into two groups: (1) those with setose pubescence and (2) those with less frequent setose pubescence (Table 1). However, in Barneby's classification (1991), only the first group was maintained in this section. The other group was recognized as section *Batocaulon*. Further, Barneby (1991: 24) proposed that section *Batocaulon* is a derivative of *Mimadenia*. Bentham's concept of section *Batocaulon* was mainly based on the presence of cauline setae and the setiform cilia on leaflet margins, instead of stamen number, which he formerly used to characterize both sections *Mimosa* and *Habbasia*. It is important to mention that there are exceptions in the species admitted by Barneby in *Batocaulon* and now, with his definition, it has become the most heterogeneous section of the genus.

Barneby's sections *Calothamnos* and *Habbasia* were postulated to be derived from section *Batocaulon*. Section *Calothamnos* (sect. *Mimosa* ser. *Lepidotae* Benth. [Table 1]) was defined by Barneby (1991) as an independent sectional rank on the basis of the stellate setae. He proposed that the stellate seta type was clearly derived from the plumose one by shortening of the primary axis and elimination of some or all of the branches. According to Barneby's position (1991), the survival of the rudimentary inner set of filaments in some species of *Calothamnos* suggests that the origin of the section could be closer to the diplostemonous and stellate flowers from section *Batocaulon* ser. *Leiocarpae*.

Although *Mimosa lanuginosa* Glaz. ex Burkart and *M. diversipila* Micheli have stellate seta indumentum, in Barneby's taxonomic classification (1991), they were excluded from section *Calothamnos* and transferred to section *Mimosa* ser. *Mimosa* subser. *Polycephalae* (Benth.) Barneby and section *Mimosa* ser. *Mimosa* subser. *Brevipedes* (Benth.) Barneby, respectively. *Mimosa lanuginosa* shares habit type and the paleaceous calyx with other members of subseries *Polycephalae*, although both features are unknown in section *Calothamnos*. In contrast, the calyx of *M. diversipila* is reduced to a rim as is the case in many species of section *Calothamnos*, but it is a virgate subshrub with mostly simple, densely foliate stems extending into long efoliate racemes of capitula, a condition absent from other members of section *Calothamnos*. Based on Barneby's proposal, the plumose indumenta present in several infrageneric groups could be considered a convergence in an evolutionary scenario.

The haplostemonous section *Mimosa* was considered to be derived from *Habbasia*. Barneby (1991) excluded series *Lepidotae* and *Spiciflorae* Benth. from section *Mimosa* (Table 1). The *Spiciflorae* species were transferred to *Batocaulon* ser. *Plurijugate* Karsten, although they have either a tetramerous or pentamerous perianth and lack the setiform trichomes characteristic of section *Mimosa* (Barneby, 1991). Section *Mimosa* sensu Bentham (1875), or Barneby (1991), shows the most derived features such as the habit (mainly subshrubs to herbs), reduction of leaf formula, craspedodrome leaflet venation, and reduction of petals and androecium numbers (Barneby, 1991: 23).

Four of the five sections recognized by Barneby (1991) are represented in southern South America: *Batocaulon*, *Habbasia*, *Calothamnos*, and *Mimosa*. During the taxonomic analysis of the species from that austral region (Fortunato, unpublished data), conflicts of delimitation were found between: (a) sections *Batocaulon* and *Habbasia*, (b) sections *Calothamnos* and *Mimosa*, and (c) among series and subseries within section *Mimosa*.

Thus, Barneby's hierarchical treatment of *Mimosa* has raised some controversial issues. In an effort to examine these, we propose to use information from genomic data, which are still lacking for *Mimosa* species. Noncoding chloroplast DNA (cpDNA) regions have been used extensively for plant phylogenetic analyses and have proven to be particularly informative at the infrageneric level or when comparing related genera (Taberlet et al., 1991; Bohle et al., 1994; Gielly & Taberlet, 1994; Sang et al., 1997; Baker et al., 1999; Murphy et al., 2000; Hughes et al., 2003; Luckow et al., 2003, 2005; Simpson et al., 2004; Jobson & Lukow, 2007).

This paper reports preliminary phylogenetic analyses of chloroplast nucleotide sequences of the *trnL* intron and the *trnL-trnF* intergenic spacer from 34 species of *Mimosa* and related genera. The main purposes of this study are to: (1) examine the evolutionary relationships within *Mimosa* and among *Mimosa* and other members of the Leguminosae; (2) determine if *Mimosa* is a monophyletic group and, in the case that it is, what the monophyletic units within the genus are; (3) determine whether the phylogeny based on *trnL* intron and the *trnL-trn*F intergenic spacer data is congruent with the current classification and the evolutionary sequence proposed (Barneby, 1991); and (4) gain further insight into the subsequent phylogenetic studies of the genus *Mimosa*.

MATERIALS AND METHODS

The *trnL* intron and *trnL-trnF* intergenic spacer regions (Taberlet et al., 1991) were sequenced for a total of 34 taxa (Table 2). We included species that represent sections *Mimosa*, *Habbasia*, *Calothamnos*, and *Batocaulon* distributed in Argentina, Paraguay, and Brazil. We analyzed both fresh leaflets that were collected and dried in the field with silica gel, and leaflets from herbarium specimens. Morphological observations for the species were made at the Instituto de Recursos Biológicos, Instituto Nacional de Tecnología Agropecuraria (INTA), Castelar (BAB) on herbarium loans from B, BA, BAA, BAF, BH, BM, CORD, CTES, E, F, G, GH, HB, K, LIL, M, MO, NY, P, PY, RB, SI, SP, US, and W. Six outgroups representing different mimosoid tribes were selected on the basis of morphological and molecular criteria (Luckow et al., 2003, 2005; Jobson & Luckow, 2007). Taxa, voucher details, and GenBank accession numbers are listed in Table 2.

Genomic DNA was isolated with a CTAB protocol (Doyle & Doyle, 1987) or with the DNA Easy Extraction kit (Qiagen, Valencia, California, U.S.A.) according to the manufacturer's instructions. Two cpDNA regions were amplified from purified DNA via polymerase chain reaction (PCR) using the four primers, c (5′-CGAAATCGGTAGACGCTACG-3′), d (5′-GGGGATAGAGGGACTTGAAC-3′), e (5′-GGTTCAAGTCCCTCTATCCC-3′), and f (5′-ATTTGAACTGGTGACACGAG-3′) (Taberlet et al., 1991). PCR reactions were of 50 µl volume, including 2.5 units of Taq-DNA polymerase (Invitrogen, Carlsbad, California, U.S.A.), 0.2 mM each dNTP (Invitrogen), 50 ng each primer (synthesized by AlphaDNA, Montreal, Canada), 3 mM $MgCl_2$ (Invitrogen), and 50 ng genomic DNA. Amplification was performed on a Biometra (Goettingen, Germany) T-gradient thermal cycler using the following steps: 95°C for 4 min., 35 cycles of 94°C for 30 sec., 55°C for 30 sec., and 72°C for 2 min., with an additional final extension step of 10 min. at 72°C. Amplified products were separated on 1% agarose Tris-acetate-ethylenediamine tetraacetic acid (TAE) gels and purified using QIAquick Gel Extraction kit (Qiagen) and used as a template for direct sequencing. In some cases, direct sequencing failed and cloning was performed using the pGEM T-Easy Vector System I (Promega, Madison, Wisconsin, U.S.A.) with DH5α competent bacterial strain. Sequencing reactions were performed with an ABI 3730 XL automatic DNA sequencer by Macrogen Inc. (Seoul, Korea). The same primers or the universal T7 and SP6 primers were used to make the primer extension for the direct sequence or cloning fragments, respectively.

Sequences were edited with the computer program BioEdit (Hall, 1999), initial alignment was performed using ClustalX version 1.8 (Thompson et al., 1997) with the default parameters, and minimal manual adjustment was made. Both DNA regions were merged in WinClada (Nixon, 1999). Uncertain positions located near the primer annealing sites and regions in which the alignment was ambiguous were excluded from the data set.

Parsimony analysis was conducted with NONA (Goloboff, 1998) included in the WinClada software (Nixon, 1999) using 1000 random addition sequences, tree bisection-reconnection (TBR) holding 100 trees per replicate, and attempting to swap to completion. Characters were considered unordered and equally weighed. The bootstrap analysis used 1000 replications each with 10 random additions holding 10 in each replicate, with a maximum of 100 trees saved per replication and mapped to the selected tree. Based on principal morphological criteria for delimitation of sections, 10 morphological characters were selected for optimization on the *trnL* intron and the *trnL-trnF* intergenic spacer phylogeny to allow for discussion of the evolution of these characters in a phylogenetic context. Morphological features (listed in Fig. 3) were scored from specimens in the collection of the BAB herbarium. Nine of these characters have two states and one is multistate.

Table 1. Bentham (1875) and Barneby (1991) taxonomic proposal in *Mimosa* L.

Bentham (1875)		Barneby (1991)		
Section	Series	Section	Series	Subseries
Habbasia DC. Setose pubescence		*Habbasia* DC., ca. 80	*Bipinnatae* DC.	
			Habbasia	
			Pachycarpae Benth.	
			Setosae Barneby	
			Neptunioideae Barneby	
			Rondonianeae Barneby	
			Rojasianae Barneby	
			Pseudocymosae Hass	
			Piresianae Barneby	
Occasional setose pubescence	*Glanduliferae* Benth.	*Mimadenia* Barneby, ca. 16	*Glanduliferae* Benth.	
			Nothacaciae Barneby	
			Revolutae Barneby	
	Rubicaules Benth.	*Batocaulon* DC., ca. 85	*Rubicaules* Benth.	
	Acanthocarpae Benth.		*Acanthocarphae* Benth.	
	Ephedroideae Benth.		*Ephedroideae* Benth.	
	Stipellares Benth.		*Stipellares* Benth.	
	Leptopodae Benth. (= Paucifoliatae Benth.)		*Paucifoliate* Benth.	
	Cesalpiniifoliae Benth.		*Cesalpiniifoliae* Benth.	
	Leptostachyae Benth. (= *Leiocarpae* Benth., *Stachyomima* Benth., *Tomentosae* Benth. sensu Bentham, 1841–1842)		*Leiocarpae* Benth.	
			Distachyae Barneby (= Leiocarpae Benth.; Grether, 2000)	
			Andinae Barneby	
			Acantholobae Barneby	
			Boreales Barneby	
			Bimucronatae Barneby	
			Eucaenioideae Barneby	
			Fagaracanthae Barneby	
			Bahamenses Barneby	
			Farinosae Barneby	
			Echinocaulae Barneby	
			Glandulosae (Benth.) Barneby	
			Auriculate Barneby	
			Ceratoniae Barneby	
			Cordistipulae Barneby	
			Campicolae Barneby	
			Filipides Barneby	
			Quadrivalves Barneby	
			Plurijugae Karsten	
Mimosa	*Lepidotae* Benth.	*Calothamnos* Barneby, ca. 24		
	Myriophyllae Benth.	*Mimosa*, ca. 180	*Myriophyllae* Benth.	
	Sensitivae Benth.		*Mimosa*	*Mimosa*
	Pectinatae Benth.			*Pectinatae* (Benth.) Barneby
	Pudicae Benth.			*Pudicae* (Benth.) Barneby
	Pedunculosae Benth.			*Pedunculosae* (Benth.) Barneby
	Meticulosae Benth.			*Dolentes* Barneby
				Polycephalae (Benth.) Barneby
	Hirsutae Benth.			*Hirsutae* (Benth.) Barneby
	Obstrigosae Benth.			*Obstrigosae* (Benth.) Barneby

Table 1. Continued.

Bentham (1875)		Barneby (1991)		
Section	Series	Section	Series	Subseries
	Castae Benth.	*Mimosa*, ca. 180		*Castae* (Benth.) Barneby
				Dolentes Barneby
				Polycarpae Barneby
				Teledactylae Barneby (= ser. *Teledactylae* (Barneby) R. Grether; Grether, 2000)
				Lactifluae Barneby (= ser. *Lactifluae* (Barneby) R. Grether; Grether, 2000)
				Bolivianae Barneby
				Lundianae Barneby
				Trichocephalae Barneby
				Ramosissimae Barneby
				Serrae Barneby
				Sparsae Barneby
				Morongianae Barneby
				Bipennatulae Barneby
				Affines Barneby
				Simplicissimae Barneby
				Dicerasteae Barneby
				Discobolae Barneby
				Brevipedes Barneby
				Thomistae Barneby
				Pogocephalae Barneby
				Microcarpae Barneby
				Lanatae Barneby
	Modestae Benth.		*Modestae* Benth.	*Macrocalycinae* Barneby
				Reptantes Barneby
				Ramnetaceae Barneby
				Axillares Barneby
				Dryandroideae Barneby
				Dutranae Barneby
				Widgrenianae Barneby
				Diffusae Barneby
	Spiciflorae Benth.	*Mimadenia* Barneby	*Myriadeniae* Barneby	
		Batocaulon DC.	*Plurijugae* Karsten	

RESULTS

The aligned length for the *trnL* and the *trnL-trnF* region is 633 bp and 514 bp, respectively. In the ingroup, DNA sequence lengths of the intron ranged from 525 bp in *Mimosa paupera* Benth. to 541 bp in *M. somnians* Humb. & Bonpl. ex Willd. The outgroup species had shorter sequences (496–524 bp). For the *trnL-trnF* intergenic spacer, DNA sequence lengths varied from 358 bp in *M. oligophylla* Micheli and *M. balansae* Micheli to 388 bp in *M. paupera*.

A matrix of 582 bp length for the *trnL* intron and 458 bp for the *trnL-trnF* intergenic spacer was analyzed. Gaps in the ingroup varied from 1 to 17 bp in length for the intron and from 1 to 36 bp for the intergenic spacer. The data matrix that was used consisted of 1040 positions, from which 124 (11.9%) were potentially informative characters. Sequence characteristics are summarized in Table 3.

Parsimony analysis resulted in 92 trees consisting of 470 steps with a consistency index (CI) of 0.68 and a retention index (RI) of 0.65, excluding uninformative characters. The majority consensus tree and one of the most parsimonious trees are shown in Figures 1 and 2, respectively. In general terms, the preferred topology is in agreement with the consensus tree. The species of genus *Mimosa* analyzed here constitute a single clade in the majority consensus tree (Fig. 1) and in the preferred topology cladogram (Fig. 2, BS =

Table 2. Species names for DNA used in the present study of *trnL* and *trnL-trnF* sequences, vouchers (deposited at BAB [Herbarium Inst. Recursos Biológicos, INTA, Argentina]), and GenBank accession numbers. Taxa are in alphabetical order. RHF = Reneé H. Fortunato; JAG = Julián A. Greppi; MAL = Melissa A. Luckow; EMZ = Elsa M. Zardini.

	Species	Herbarium voucher	*trnL* GenBank numbers	*trnL-trnF* GenBank numbers
	Mimosa adenotricha Benth.	RHF 8450	DQ344579	DQ344613
	Mimosa balansae Micheli	RHF 7534	DQ344552	DQ344585
	Mimosa bifurca Benth. var. *bifurca*	RHF 7556	DQ344553	DQ344586
	Mimosa bonplandii (Gillies ex Hook. & Arn.) Benth.	JAG 92	DQ344581	DQ344615
	Mimosa brevipetiolata Burkart	JAG 127	DQ344582	DQ344616
	Mimosa candollei R. Grether	RHF 7555	DQ344555	DQ344588
	Mimosa debilis Humb. & Bonpl. ex Willd.	RHF 8085	DQ344561	DQ344594
	Mimosa detinens Benth.	MAL 4491	DQ344558	DQ344591
	Mimosa diversipila Micheli var. *diversipila*	RHF 8810	DQ344584	DQ344618
	Mimosa flagellaris Benth.	RHF 7887	DQ344557	DQ344590
	Mimosa hexandra Micheli	MAL 4584	DQ344556	DQ344589
	Mimosa hirsutissima Mart.	RHF 7962	DQ344562	DQ344595
	Mimosa leimonias Barneby & Fortunato	EMZ 41158	DQ344575	DQ344609
	Mimosa maguirei Barneby	RHF 8418	DQ344576	DQ344610
	Mimosa obstrigosa Burkart	RHF 8077	DQ344568	DQ344601
	Mimosa oligophylla Micheli	RHF 8074	DQ344574	DQ344608
	Mimosa paupera Benth.	RHF 8018	DQ344565	DQ344598
	Mimosa pigra L.	JAG 38	DQ344560	DQ344593
	Mimosa pilulifera Benth.	JAG 39	DQ344573	DQ344607
	Mimosa polycarpa Kunth	RHF 8019	DQ344566	DQ344599
	Mimosa radula Benth.	RHF 8413	DQ344577	DQ344611
	Mimosa sensibilis Griseb.	RHF 8385	DQ344580	DQ344614
	Mimosa setosa Benth. var. *setosa*	RHF 8445	DQ344578	DQ344612
	Mimosa somnians Humb. & Bonpl. ex Willd.	RHF 7953	DQ344563	DQ344596
	Mimosa strigillosa Torr. & A. Gray	RHF 8949	DQ344567	DQ344600
	Mimosa tweedieana Barneby ex Glazier & Mackinder	RHF 7949	DQ344572	DQ344606
	Mimosa uliginosa Chodat & Hassl.	RHF 8059	DQ344564	DQ344597
	Mimosa xanthocentra Mart. var. *xanthocentra*	RHF 7650	DQ344559	DQ344592
Outgroup taxa	*Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul	RHF 7583	DQ344571	DQ344605
	Calliandra tweediei Benth.	RHF 8853	DQ344583	DQ344617
	Mimozyganthus carinatus (Griseb.) Burkart	RHF 7567	DQ344570	DQ344604
	Neptunia pubescens Benth.	RHF 7923	DQ344551	DQ344603
	Parapiptadenia excelsa (Griseb.) Burkart	RHF 7669	DQ344569	DQ344602
	Piptadenia viridiflora (Kunth) Benth.	RHF 7586	DQ344554	DQ344587

80%), indicating that this group is monophyletic. Both cladograms indicate that *Piptadenia viridiflora* (Kunth) Benth. is the species most closely related to *Mimosa* (Fig. 2, BS = 87%).

In both trees, the species of section *Batocaulon* are not clustered together, and *Mimosa hexandra* Micheli and *M. detinens* Benth. are separated from the rest and constitute a basal clade (Fig. 2, BS = 94%). The

Table 3. Sequence characteristics for the *trnL* intron and the *trnL-trnF* intergenic spacer sequenced in this study.

	trnL intron	*trnL-trnF* intergenic spacer	Total
Length range (bp)	496–541	358–388	—
Aligned length (bp)	633	514	1147
No. of sites excluded (bp)	51	56	107
Analyzed region (bp)	582	458	1040
Indels	27	26	53
Size of indels (ingroup) (bp)	1–17	1–36	1–36
Base substitutions	31	40	71
Total potentially informative characters	58	66	124

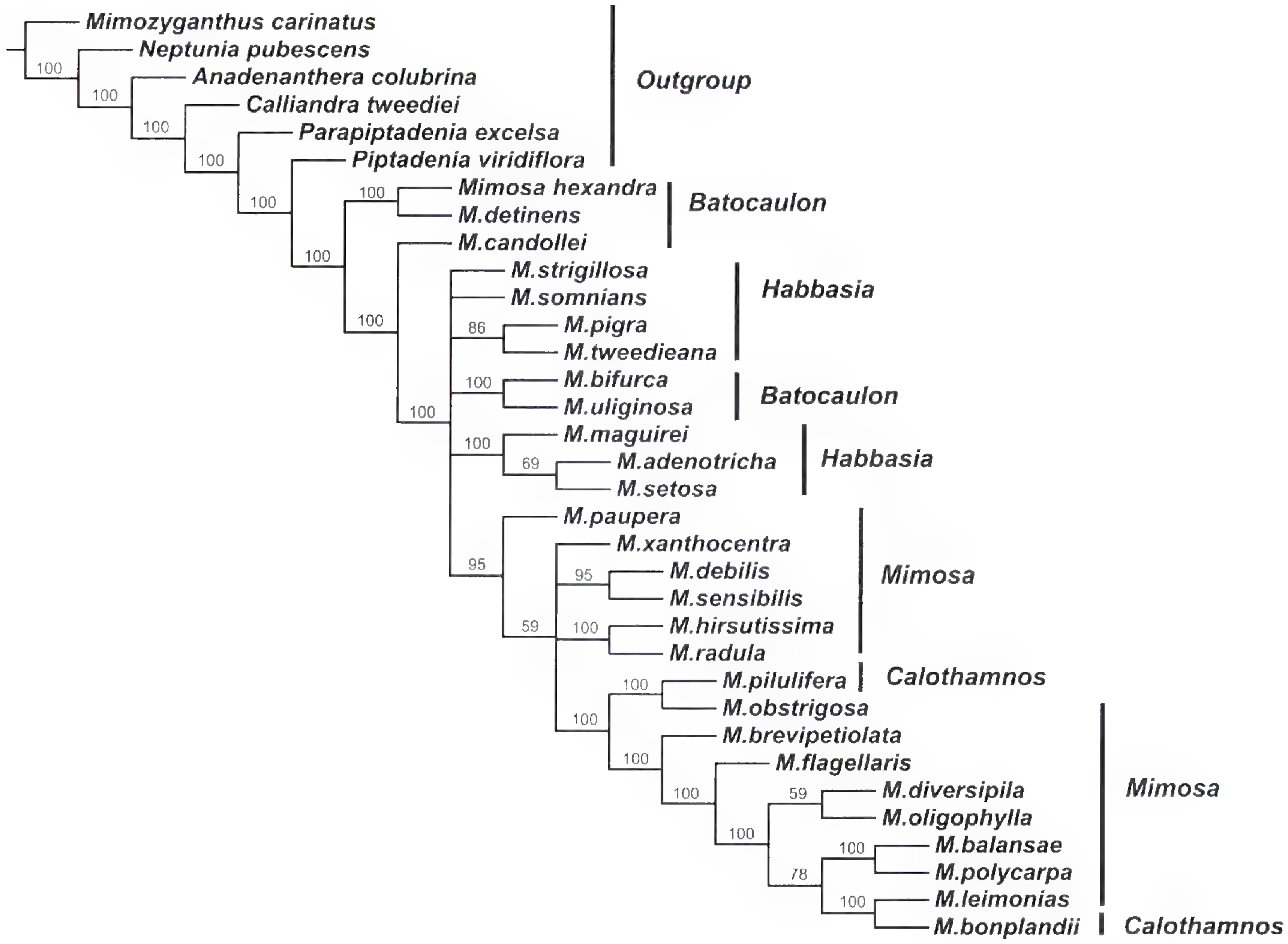


Figure 1. Majority consensus tree obtained from 92 equally parsimonious trees (length 470, CI = 0.68, RI = 0.65) based on *trnL* intron and *trnL-trnF* intergenic spacer sequence data. Numbers above branches are the percentage of trees in which the clade is supported. The sections of the genus are indicated according to Barneby (1991).

remaining species of section *Batocaulon*, *M. uliginosa* Chodat & Hassl., and *M. bifurca* Benth., are placed with the species of section *Habbasia*. From the polymorphic section *Batocaulon*, *M. candollei* R. Grether shares more characters (Fig. 2, BS = 80%) with section *Habbasia* than do *M. hexandra* and *M. detinens*. In Figure 2, *M. bifurca* and *M. uliginosa* are more recently differentiated and clustered with high bootstrap support within section *Habbasia* (Fig. 2, BS = 99%). However, this last clade is not highly supported (Fig. 2, BS < 50%) and can partially explain the polytomy found in the majority consensus tree (Fig. 1). *Mimosa maguirei* Barneby, *M. adenotricha* Benth., and *M. setosa* Benth. (sect. *Habbasia* ser. *Pachycarpae* Benth.) are clustered (Figs. 1, 2, BS = 94%), and the relation among clades integrated by representatives from *Batocaulon* and *Habbasia* is not solved (Fig. 1). On the other hand, the preferred topology (Fig. 2) indicates that the *M. maguirei*, *M. adenotricha*, and *M. setosa* clade is sister in relation to the cluster constituted by *M. tweedieana* Barneby ex Glazier & Mackinder and *M. pigra* L. (sect. *Habbasia* ser. *Habbasia*), *M. strigillosa* Torr. & A. Gray (sect. *Habbasia* ser. *Habbasia*), and *M. somnians* (sect. *Habbasia* ser. *Bipinnatae*) (Fig. 2).

In both figures, the species of sections *Mimosa* and *Calothamnos* constitute a single clade. In Figure 1, *Mimosa paupera* is sister to the remaining species; however, in the consensus tree (Fig. 2), this species is sister to the clade formed by *M. hirsutissima* Mart. and *M. radula* Benth. In a similar way, *M. xanthocentra* Mart. is sister (Fig. 2, BS < 50%) to the clade constituted by *M. debilis* Humb. & Bonpl. ex Willd. and *M. sensibilis* Griseb. (Fig. 2, BS = 71%). In the consensus tree, *M. xanthocentra*, the cluster formed by *M. debilis* and *M. sensibilis*, the cluster formed by *M. hirsutissima* and *M. radula*, and the group that includes the remaining species from sections *Mimosa* and *Calothamnos* that were analyzed constitute a polytomy. A cluster formed by *M. pilulifera* Benth. (sect. *Calothamnos*) and *M. obstrigosa* Burkart (sect. *Mimosa*) can be seen in both trees. From the remaining species, the same topology is found in both trees (Figs. 1, 2). *Mimosa brevipetiolata* Burkart is basal (Fig. 2, BS = 71%), followed by *M. flagellaris* Benth. (Fig. 2, BS = 79%), and a group that is split into two clades (Fig. 2, BS = 72%). The first one (weakly supported) consisted of *M. diversipila* and *M. oligophylla*. The second is a clade (Fig. 2, BS = 50%) formed by two groups; the

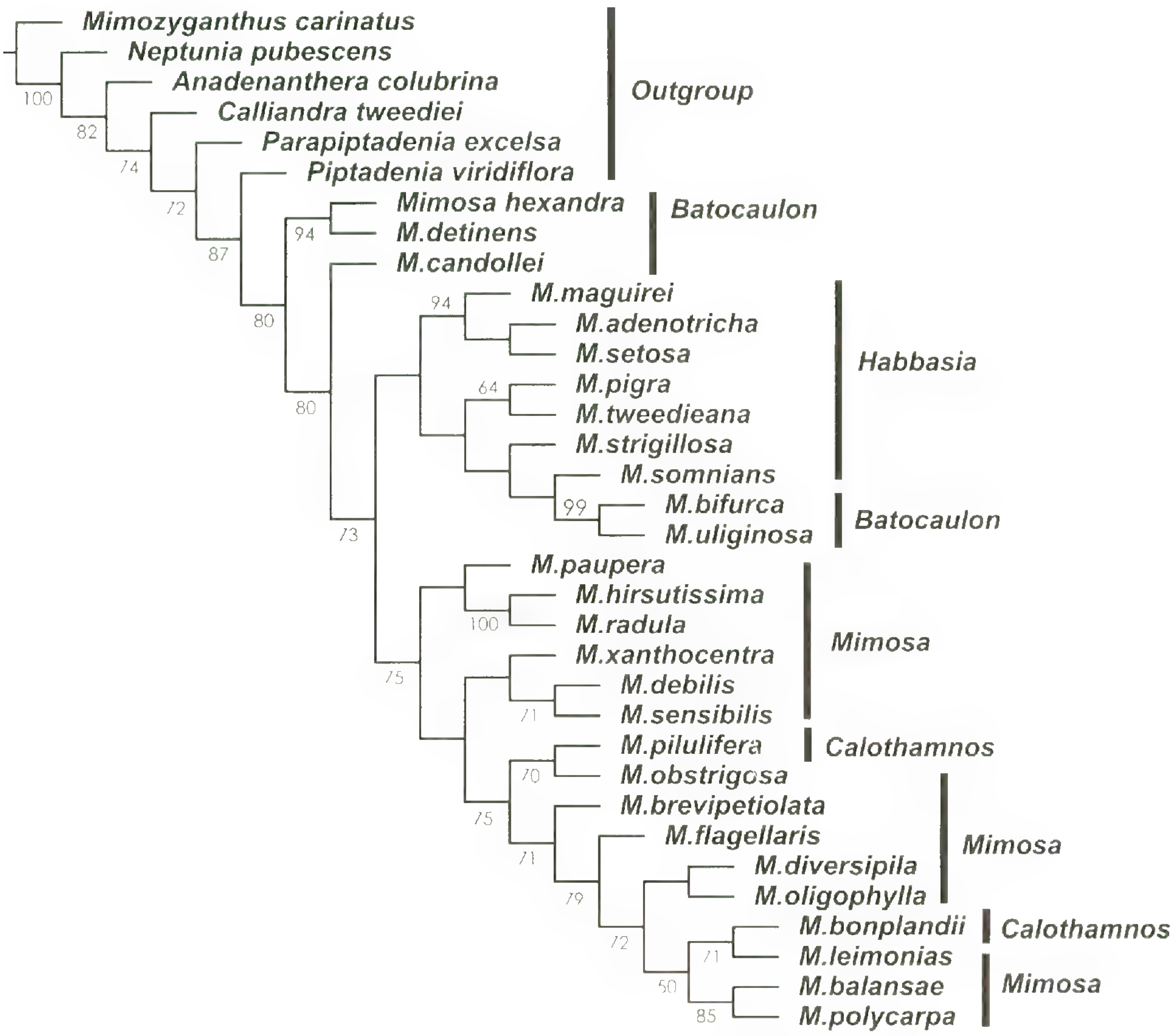


Figure 2. One of the most parsimonious trees of 470 steps based on *trnL* intron and *trnL-trnF* intergenic spacer sequence data. Bootstrap values greater than 50% are shown at the nodes. The sections of the genus are indicated according to Barneby (1991).

first one (Fig. 2, BS = 71%) includes *M. bonplandii* (Gillies ex Hook. & Arn.) Benth. (sect. *Calothamnos*) and *M. leimonias* Barneby & Fortunato (sect. *Mimosa*), and the second includes *M. balansae* and *M. polycarpa* Kunth (Fig. 2, BS = 85%), both from section *Mimosa*.

DISCUSSION

The present study represents the first molecular approach toward a phylogeny of *Mimosa*. This is a preliminary reconstruction based on the *trnL* intron and *trnL-trnF* intergenic spacer, including species from southern South America. Although sampling of taxa is limited, the four sections found in the southern center of diversity of the genus (south of Amazonia in Brazil and adjacent areas of Paraguay, Argentina, and Uruguay) (Barneby, 1991) are represented. Noncoding regions have been presumed to be more useful at lower taxonomic ranks because they are less functionally constrained and are free to vary, thereby potentially providing more phylogenetically informative characters per unit of sequencing effort (Clegg et al., 1994; Gonzalez & Vovides, 2002). In *Mimosa*, both the *trnL* intron and the *trnL-trnF* intergenic spacer exhibited a similar level of informative characters (12% on average) to most of the other plant species assayed with comparable methods (Baker et al., 1999; Bayer et al., 2000; Murphy et al., 2000; Gonzalez & Vovides, 2002). Despite the fact that the ambiguous regions for the alignments were excluded, a large data set (1040 characters) was obtained, and 124 informative sites could be retrieved for the sampled species. A low level of conflict among data ensured that many of the relationships recovered were highly supported and are addressed in this contribution.

The cpDNA allowed us to make a phylogenetic hypothesis. The cladogram indicates that the four sections of *Mimosa* included in this study may be considered a monophyletic taxon, sister to *Piptadenia viridiflora* (Fig. 2, BS = 80%). As discussed in the introduction, conflicts of delimitation were found between (a) sections *Batocaulon* and *Habbasia*, (b) sections *Calothamnos* and *Mimosa*, and (c) among series and subseries within section *Mimosa*, and are discussed below.

SECTIONS *BATOCAULON* AND *HABBASIA*

Section *Batocaulon* was defined as a highly polymorphic group (Barneby, 1991) mainly based on plain, cauline setae and setiform cilia on leaflet margins. However, these types of indumenta are also found in some representatives of sections *Habbasia* and *Mimosa*. The species analyzed here are grouped into two clusters; the first one includes *M. detinens* and *M. hexandra* (basal and highly supported), and the second includes *M. bifurca* and *M. uliginosa* (more recent and also highly supported). Our analysis suggests that species of section *Batocaulon* may have arisen from two speciation events; the first one gave the series *Farinosae* Benth. (*M. detinens*) and *Bimucronatae* Barneby (*M. hexandra*), and a later event gave rise to series *Stipellares* (*M. bifurca* and *M. uliginosa*). This result indicates that the section *Batocaulon* recognized by Barneby (1991) cannot be considered a natural group.

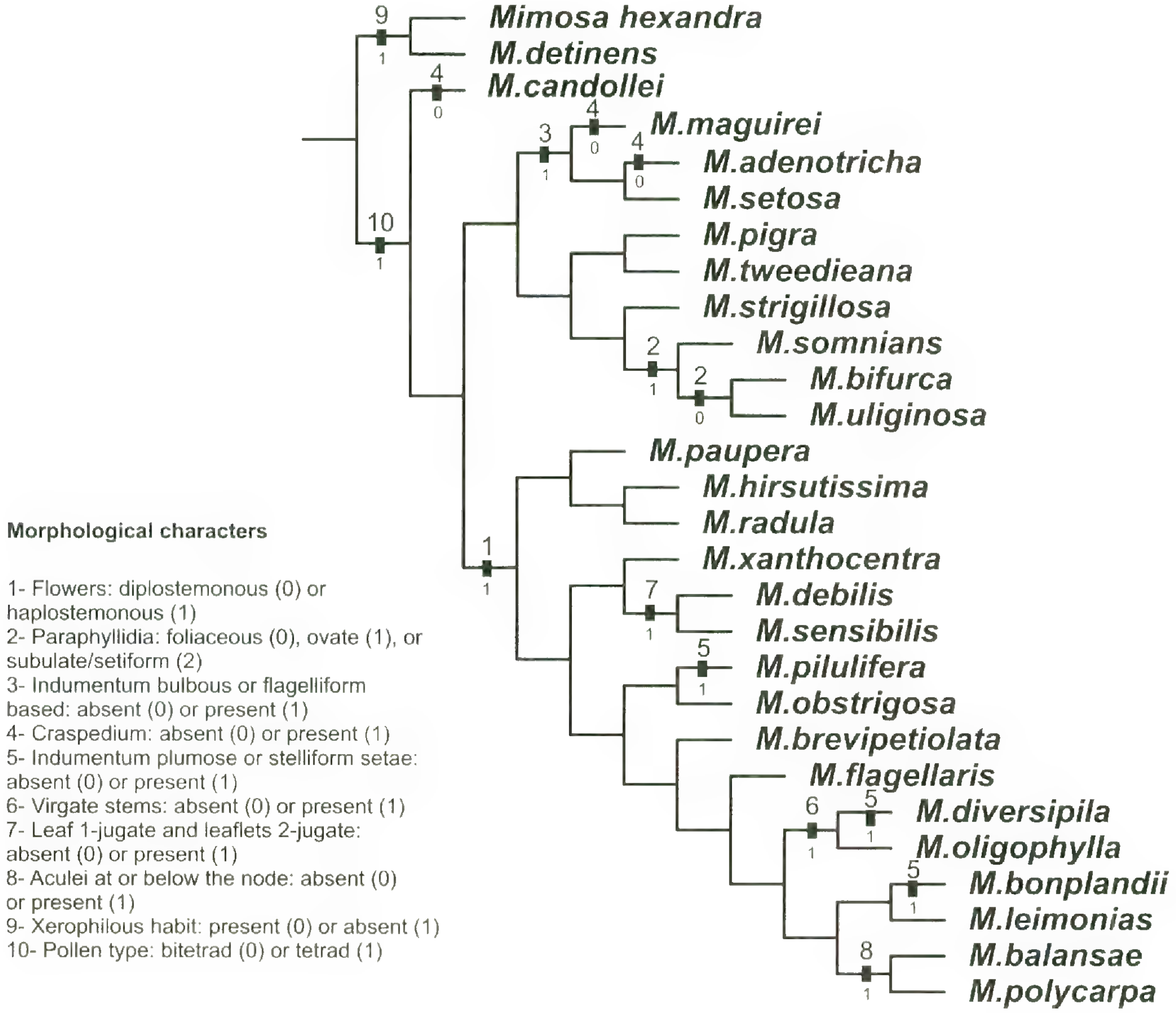
The position in the tree for *Mimosa detinens* and *M. hexandra* can be partially explained by the xerophilous habit and the bitetrad type pollen (Caccavari, 1985, 1986a, b, 1989; Martínez-Bernal et al., 2005) as shown by the optimization in the phylogeny hypothesis indicated in Figure 3 (characters 9 and 10). Moreover, the association between *M. detinens* and *M. hexandra* could also be explained by the flower's white filament (Burkart, 1948; Barneby, 1991). Series *Stipellares* is characterized by its particular foliar morphology having paraphyllidia at the base of pinna-rachis elliptic, reniform to suborbicular, simulating diminutive leaflets; no interpinnal spicules; and, in some species, pinnae and leaflets alternately inserted along the leaf axes. We mapped three types of paraphyllidia (Fig. 3, character 2) and determined that the foliaceous type could be considered a derived feature from the ovate and subulate types.

Within the clade in which all species of section *Habbasia* sensu Barneby are represented together along with section *Batocaulon* ser. *Stipellares*, two clades may be distinguished (Figs. 1, 2). The first includes the species of series *Pachycarpae* (*Mimosa maguirei*, *M. adenotricha*) and series *Setosae* (*M. setosa*). Barneby described the series *Setosae* in order to include the polymorphic *M. setosa* (1991: 352–353), which shows transitional traits between sections *Habbasia* and *Batocaulon*, but exhibits articulated pods with relatively narrow replum that differentiate it from those of series *Pachycarpae*. Although we include few representatives of series *Pachycarpae* and *Setosae*, the molecular results presented here suggest maintaining them as a single series. When the indumentum type typical of both series was mapped (Fig. 3, character 3), the bulbosus or flagelliform type appears at the base of the clade integrated by *M. maguirei*, *M. adenotricha*, and *M. setosa*; however, one might assume a parallel derivation of the valvate fruit type in *M. adenotricha*, *M. maguirei*, and *M. candollei* (Fig. 3, character 4).

In Figure 2, *Mimosa tweedieana* and *M. pigra* constituted a moderately supported clade (BS = 64%). Nevertheless, although it is in the same series, *M. strigillosa* is placed in another group. *Mimosa strigillosa* differs from other members of series *Habbasia* by its herbaceous life form, with stems humifuse, radicant; basally monadelphous stamens; and smaller, 2- to 5-seeded pods. Moreover, this species has a bicentric distribution (southeastern U.S.A. to northeastern Mexico and the basins of the Paraná and Paraguay rivers in Paraguay to northeastern Argentina and western Uruguay) that is unusual in the remaining species of series *Habbasia*. Although in the majority consensus tree (Fig. 1) it is not solved, in the selected phylogeny hypothesis (Fig. 2), *M. strigillosa* is closely related to *M. somnians* (*Bipinnatae*); despite this, the clade is weakly supported. The association between the latter species and the taxa included from section *Batocaulon* ser. *Stipellares* (*M. bifurca* and *M. uliginosa*) is also weak. However, this latter relation may be partially explained by the absence of interpinnal spicules and the plausible progression of paraphyllidia morphology (Fig. 3, character 2). Given that all the species of series *Bipinnatae* have striate nerved corollas not found in other members of *Habbasia* species, one might hypothesize that it is a natural group. Nevertheless, the tendency could not be tested in this study based on the limited number of taxa included.

SECTIONS *MIMOSA* AND *CALOTHAMNOS*

In our phylogenetic hypothesis, the species of sections *Mimosa* and *Calothamnos* are derived from a common ancestor (Figs. 1, 2). The position of the *Calothamnos* species can be explained by the presence of haplostemonous flowers (Fig. 3, character 1) as was proposed by Bentham (1841–1842, 1875). Although previous works (Grether et al., 2005) confirmed the monophyly of section *Calothamnos*, in our study, the two representatives of section *Calothamnos* analyzed are not clustered together. It may be that the section is underrepresented, but this analysis indicates that section *Calothamnos* is not monophyletic. The haplostemonous species with the indumentum plumose or consisting of stelliform setae were recognized by Bentham (1841) as section *Mimosa* ser. *Lepidotae* and transferred by Barneby (1991) to a new section *Calothamnos* (Table 1). However, when the indumentum plumose or stelliform setae trait is mapped onto the



Morphological characters

1- Flowers: diplostemonous (0) or haplostemonous (1)
2- Paraphyllidia: foliaceous (0), ovate (1), or subulate/setiform (2)
3- Indumentum bulbous or flagelliform based: absent (0) or present (1)
4- Craspedium: absent (0) or present (1)
5- Indumentum plumose or stelliform setae: absent (0) or present (1)
6- Virgate stems: absent (0) or present (1)
7- Leaf 1-jugate and leaflets 2-jugate: absent (0) or present (1)
8- Aculei at or below the node: absent (0) or present (1)
9- Xerophilous habit: present (0) or absent (1)
10- Pollen type: bitetrad (0) or tetrad (1)

Figure 3. Optimization of 10 morphological characters over the preferred topology. Changes are represented by boxes. Above branches, numbers indicate the characters according to the list, while the trait states are indicated below.

tree, a parallel derivation might also be considered (Fig. 3, character 5), indicating that these characters are of limited phylogenetic value.

Mimosa pilulifera (sect. *Calothamnos*) constitutes a clade with *M. obstrigosa* (ser. *Mimosa* subser. *Obstrigosae* (Benth.) Barneby), and *M. bonplandii* (sect. *Calothamnos*) is clustered with *M. leimonias* (Fig. 2, BS = 71%) (ser. *Mimosa* subser. *Pedunculosae* (Benth.) Barneby). The yielded groups are unexpected because these species exhibit different morphological characteristics, such as the type of indumentum (branched trichomes for *M. pilulifera* and *M. bonplandii*, retrorsely apressed setae for *M. obstrigosa*, and glabrous to setulose-ciliolate for *M. leimonias*), life form (shrub in *M. pilulifera*, *M. bonplandii*, and *M. obstrigosa* vs. herb in *M. leimonias*), division of leaves (pinnae 1-jugate in *M. leimonias*, *M. pilulifera*, and *M. obstrigosa* vs. pinnae 2- to 9-jugate in *M. bonplandii*), and androecium type and color of the filament (monadelphous and pale yellow in *M. bonplandii* vs. filaments free to the base and pink in the remaining species). The results suggest that these traits also exhibit low value from a phylogenetic standpoint.

As pointed out in the introduction, *Mimosa diversipila* shares the calyx and pubescence types with species of section *Calothamnos*, and has the virgate life form present in section *Mimosa* ser. *Mimosa* subser. *Brevipedes* (Barneby, 1991: 708–710). In cladograms, *M. diversipila* is clustered with *M. oligophylla* from section *Mimosa* ser. *Mimosa* subser. *Pedunculosae*. Although this association is weak, it can be partially expected because both show the simple virgate habit absent from the remaining species from subseries *Pedunculosae* analyzed here (Fig. 3, character 6).

SERIES AND SUBSERIES OF SECTION *MIMOSA*

Two well-supported groups are obtained: in the first, the species of subseries *Mimosa* (*M. debilis* and *M. sensibilis*) are clustered together in accordance with the Bentham (1875) (series *Sensitivae* Benth.) and Barneby (1991) subdivision based on the pinna 1-

Table 4. List of *Mimosa* species sequenced for this study. Taxa are organized according to Barneby's classification (1991).

Barneby (1991)	Species
Sect. *Habbasia* ser. *Bipinnatae*	*Mimosa somnians* Humb. & Bonpl. ex Willd.
Sect. *Habbasia* ser. *Habbasia*	*Mimosa strigillosa* Torr. & A. Gray
Sect. *Habbasia* ser. *Habbasia*	*Mimosa tweedieana* Barneby ex Glazier & Mackinder
Sect. *Habbasia* ser. *Habbasia*	*Mimosa pigra* L.
Sect. *Habbasia* ser. *Pachycarpae*	*Mimosa adenotricha* Benth.
Sect. *Habbasia* ser. *Pachycarpae*	*Mimosa maguirei* Barneby
Sect. *Habbasia* ser. *Setosae*	*Mimosa setosa* Benth. var. *setosa*
Sect. *Batocaulon* ser. *Stipellares*	*Mimosa uliginosa* Chodat & Hassl.
Sect. *Batocaulon* ser. *Stipellares*	*Mimosa bifurca* Benth.
Sect. *Batocaulon* ser. *Farinosae*	*Mimosa detinens* Benth.
Sect. *Batocaulon* ser. *Bimucronatae*	*Mimosa hexandra* Micheli
Sect. *Mimosa* ser. *Mimosa* subser. *Brevipedes*	*Mimosa diversipila* Micheli var. *diversipila*
Sect. *Mimosa* ser. *Mimosa* subser. *Hirsutae*	*Mimosa hirsutissima* Mart.
Sect. *Mimosa* ser. *Mimosa* subser. *Mimosa*	*Mimosa debilis* Humb. & Bonpl. ex Willd.
Sect. *Mimosa* ser. *Mimosa* subser. *Mimosa*	*Mimosa sensibilis* Griseb.
Sect. *Mimosa* ser. *Mimosa* subser. *Obstrigosae*	*Mimosa obstrigosa* Burkart
Sect. *Mimosa* ser. *Mimosa* subser. *Pedunculosae*	*Mimosa brevipetiolata* Burkart
Sect. *Mimosa* ser. *Mimosa* subser. *Pedunculosae*	*Mimosa flagellaris* Benth.
Sect. *Mimosa* ser. *Mimosa* subser. *Pedunculosae*	*Mimosa leimonias* Barneby & Fortunato
Sect. *Mimosa* ser. *Mimosa* subser. *Pedunculosae*	*Mimosa oligophylla* Micheli
Sect. *Mimosa* ser. *Mimosa* subser. *Polycarpae*	*Mimosa balansae* Micheli
Sect. *Mimosa* ser. *Mimosa* subser. *Polycarpae*	*Mimosa polycarpa* Kunth
Sect. *Mimosa* ser. *Mimosa* subser. *Polycephalae*	*Mimosa radula* Benth.
Sect. *Mimosa* ser. *Mimosa* subser. *Pudicae*	*Mimosa xanthocentra* Mart. var. *xanthocentra*
Sect. *Mimosa* ser. *Mimosa* subser. *Reptantes*	*Mimosa paupera* Benth.
Sect. *Calothamnos*	*Mimosa bonplandii* (Gillies ex Hook. & Arn.) Benth.
Sect. *Calothamnos*	*Mimosa pilulifera* Benth.
Sect. *Batocaulon* ser. *Quadrivalves*	*Mimosa candollei* R. Grether

jugate and leaflet 2-jugate present in all members of subseries *Mimosa* (Fig. 3, character 7). The second group is formed by *M. balansae* and *M. polycarpa*, both from subseries *Polycarpae* Barneby, which share some common traits, in particular the aculei at or below the nodes (Fig. 3, character 8). Because the species of subseries *Polycarpae* are at the tip in the molecular tree, it is suggested that they are the most recently differentiated group.

However, the position obtained for the species of section *Mimosa* does not agree completely with Barneby's classification. Examples of these discordances are the groupings of *M. hirsutissima* and *M. radula* that constitute a highly supported clade (Fig. 2, BS = 100%), although the first one belongs to subseries *Hirsutae* (Benth.) Barneby and the second to subseries *Polycephalae* (Fig. 2, Table 4). The species from subseries *Pedunculosae* (*M. flagellaris*, *M. oligophylla*, *M. brevipetiolata*, and *M. leimonias*) are not clustered, which shows that this subseries is an artificial group (Figs. 1, 2).

The low support of some clades confirms the idea that *Mimosa* is a recently diverged genus. Low divergence is expected in neutral markers, such as cpDNA introns and intergenic spacers that would not have had enough time to be fixed in different species and yield poorly supported nodes (Soltis & Soltis, 1998). Alternative explanations that cannot be ruled out are ancestral polymorphism in cpDNA or past introgression events. The latter, combined with strong directional selection in certain environments creating morphological divergence despite gene flow as postulated by Orr and Smith (1998), seems also to be a plausible explanation for *Mimosa*. In the center of diversity in south Amazonia in Brazil and adjacent areas in Paraguay, Argentina, and Uruguay, high hybridization among species from sections *Batocaulon* and *Mimosa* is described (Morales et al., 2007; Fortunato, unpublished data). The occurrence of natural hybrids followed by stabilization processes is necessary in speciation by hybridization (Grant, 1971), so the hybrids in the wild can be interpreted as evidence to suggest that interspecific hybridization plays an important role in the evolution of the genus *Mimosa*. Moreover, different ploidy levels were described in *Mimosa* in ca. 30 species (Withus & Berger, 1947; Goldblatt, 1981; Seijo, 1993, 1999, 2000; Morales et al., 2007). Morphological, cytogenetic, and molecular criteria indicated that hybridization and polypoloidy processes have been important mechanisms in the evolution of other legumes (Hughes et al., 2002). However, a study on the relative importance of each process that could explain the evolution of *Mimosa* is still lacking.

FINAL REMARKS

In this paper, we tested the monophyly of *Mimosa* and determined that it is a genus derived from *Piptadenia viridiflora*. Recently, Jobson and Luckow (2007) suggested that *P. viridiflora* should be removed from the genus *Piptadenia* based on chloroplast genes *trnL-trnF* and *trnK/matK*. Although representatives from section *Mimadenia* were not included in this study, representatives from sections *Batocaulon*, *Habbasia*, *Mimosa*, and *Calothamnos* constitute a single clade. Moreover, the sections analyzed here, accepted by Barneby (1991), are not monophyletic; in this regard, the only species that constitute a well-supported clade are those from sections *Mimosa* and *Calothamnos*. The most recent group exhibits the derived morphological features, as was proposed by Barneby (1991). The evolutionary sequence can be interpreted as a progressive reduction—from diplostemonous and free filaments to haplostemonous and an androecium with monadelphous filaments—in leaf formula, in habit life form (trees and shrubs to herb), and in pollen type (bitetrads to tetrads). However, in order to determine whether this molecular hypothesis is congruent with Barneby's proposal for relationships, a study adding representatives from *Mimadenia* is needed.

To conclude, ours is the first documented molecular study of the genus *Mimosa*. The cpDNA regions examined here provide sufficient information to resolve many relationships within the genus. This hypothesis, based on *trnL* and *trnL-trnF* intergenic spacer regions, constitutes a starting point for further analysis. It will be interesting to see whether more exhaustive sampling and additional genetic evidence (i.e., nuclear evidence or other cpDNA regions) will support the working hypothesis developed in this study.

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